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Ecology and biogeochemistry of the Antarctic Circumpolar Current during austral spring: a summary of Southern Ocean JGOFS cruise ANT X/6 of R.V. *Polarstern*

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Abstract—The R.V. *Polarstern* cruise ANT X/6, part of the international Southern Ocean JGOFS programme, investigated phytoplankton spring bloom development and its biogeochemical effects in different water masses of the Atlantic sector of the Southern Ocean: the Polar Frontal region (PFr), the southern Antarctic Circumpolar Current zone (sACC), its boundary with the Weddell Gyre (AWB) and the marginal ice zone (MIZ). The relative roles of physical stability, iron limitation and grazing pressure in enhancing or constraining phytoplankton biomass accumulation were examined. Three sections were carried out between the PFr and the ice edge along the 6°W meridian from early October to late November 1992. This paper summarises the major findings of the cruise and discusses their implications for our understanding of Southern Ocean ecology and biogeochemistry. A major finding was the negligible build-up of plankton biomass and concomitant absence of CO_2 drawdown associated with seasonal retreat of the ice cover. In striking contrast to this unexpected poverty of both the MIZ and the frontal region of the AWB, distinct phytoplankton blooms, dominated by different diatom species, accumulated in the PFr. Chlorophyll stocks in the sACC remained monotonously low throughout the study. Our findings confirm those of other studies that frontal regions are the major productive sites in the Southern Ocean and that input of meltwater and associated ice algae to the surface layer from a retreating ice edge is by itself an insufficient condition for induction of phytoplankton blooms. The blooms in the PFr developed under conditions of shallow mixing layers, high iron concentrations and relatively low grazing pressure. However, in all three blooms, high biomass extended to deeper than 70 m, which cannot be explained by either *in situ* growth or sinking out of a part of the population from the upper euphotic zone. Subduction of adjoining, shallower layers to explain depth distribution is invoked. Despite a clear CO_2 drawdown in the Polar Frontal region, the highly variable conditions encountered render reliable estimation of annual CO_2 fluxes in the Southern Ocean difficult.

INTRODUCTION

It is increasingly recognised that the vast area of the Southern Ocean includes distinct biogeochemical provinces that differ on the basis of hydrography and ecology. This has led to a suite of focused studies carried out in the framework of the international Joint Global Ocean Flux Study (JGOFS) addressing, primarily, plankton dynamics and biogeochemical cycling of carbon in different regions of the Southern Ocean (Bathmann *et al.*, in press). The cruise ANT X/6 of R.V. *Polarstern*, termed "Spring at the Ice Edge", was part of the

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European contribution to Southern Ocean JGOFS. The aim was to investigate phytoplankton spring development at the retreating marginal ice zone (MIZ), in the Antarctic Circumpolar Current (ACC), and at its fronts in order to assess the role of these distinct regions in air/sea exchange of carbon dioxide.

It has become widely accepted that the seasonal retreat of the ice cover induces rapid phytoplankton growth in the melt-water zone (Smith and Nelson, 1986; Sullivan *et al.*, 1988; Knox, 1994). Most studies of this environment have been carried out in regions influenced by coastal areas of the Antarctic Peninsula or by high inputs of melting ice such as at the Weddell/Scotia Sea Confluence (Sullivan *et al.*, 1993). Apart from such melt-water stabilisation, Hart (1934, 1942) had hypothesised that the greater productivity of coastal i.e. "*neritic*" waters could be due to higher concentrations of dissolved iron brought in from continental margins. This has been recently confirmed (Martin *et al.*, 1990; Nolting *et al.*, 1991; Westerlund and Öhmann, 1991). Therefore, it was our intention to study ecological and biogeochemical processes in the MIZ in a remote area far from the influence of continental margins. Accordingly, the eastern sector of the Atlantic was chosen as the study site. Another target of this cruise was the investigation of elevated phytoplankton stocks at the Polar Front occasionally seen in satellite images (Comiso and Maynard, 1990).

The cruise covered the period from early October (the onset of large-scale ice melt) to mid-November. The intention was to conduct transects extending from the ice edge of the eastern Weddell Sea, across the southern branch of the ACC into the Polar Frontal Zone. Time stations following drifting sediment traps were to be occupied in appropriate localities. Research projects included many individual specialities and experiments in addition to covering 24 core parameters of the Southern Ocean JGOFS protocol (Table 1).

The following processes involved in carbon cycling between the atmosphere and ocean were studied: CO_2 uptake by photosynthesis of phytoplankton in surface layers; various processes mediating recycling and modification of this organic matter; vertical flux and sequestration of carbon in the ocean interior and the deep-sea floor. Also assessed were biomass, species composition and growth rates of the major ecosystem components—phytoplankton, bacteria, protozoo- and metazooplankton—in relation to their physical and chemical environment. The abundance of birds and mammals in the study area also was determined. The investigations involved field measurements and experiments onboard ship.

Apart from the 22 research articles published in this issue, three additional articles based on data from the cruise have appeared elsewhere (Crawford, 1995; de Baar *et al.*, 1995; Jochem *et al.*, 1995). The combined database is available in the enclosed CD-ROM format and is summarised by Rommets *et al.* (1997).

Definition of hydrographic provinces

The transects between 48°S and 60°S crossed various hydrographic zones, which are referred to in the individual articles of this Special Issue. Therefore, these geographic/hydrographic zones and boundaries are defined below.

The major current jets within the broad eastward-flowing Antarctic Circumpolar Current (ACC) are associated with, from north to south, the Subantarctic Front (SAF), the Polar Front (PF), the southern ACC Front (sF) also termed Southern Polar Front (Veth *et al.*, 1997) and the ACC–Weddell Gyre Boundary (AWB) (Fig. 1). The Polar Frontal Zone (PFZ) is the zone between the Subantarctic Front and the Polar Front (Peterson and Stramma, 1991).

Table 1. *The* 20 *regular and five special Southern Ocean core activities of JGOFS. Except for moored sediment traps (*20*) the remaining* 24 *activities were all carried out during ANT X/6, with several additional field measurements and shipboard experiments. The methods as reported in individual research articles are compatible with or adjusted after JGOFS protocols. The enclosed CD-ROM (Rommets et al.,* 1997*) contains information of all activities with their investigators and methods, as well as the available data*

1. Meteorology and positioning.
2. CTD, O_2-probe, fluorometry, turbidity, Underway salinity, temperature, fluorometry.
3. Dissolved oxygen.
4. Nutrients.
5. Optics.
6. Carbon dioxide system.
7. POC and PON.
8. DOC and DON by HTCO methods.
9. Chlorophyll and pigments with HPLC.
10. Bacteria biomass and production.
11. Mesozooplankton (incl. egg production).
12. Microplankton abundance; autotrophs, heterotrophs; incl. nanoplankton.
13. Primary production by ^{14}C.
14. Primary production by O_2; only at one drift station).
15. New production with ^{15}N and export production with ^{234}Th.
16. Autotrophic pico-nano-plankton (including cyanobacteria).
17. Grazing by mesozooplankton.
18. Grazing by microzooplankton and nanozooplankton.
19. Drifting shallow sediment traps.
20. (Deep moored sediment traps; not done.)
21. Ice coverage.
22. Ice physics.
23. Ice biology.
24. Silica biogeochemical cycling.
25. Iron–plankton interactions.

The PF is commonly defined as a rather sharp transition, most notably in temperature. However, the PF is highly dynamic and is associated with numerous convolutions and eddies covering a wider latitudinal range of about three degrees (Veth *et al.*, 1997). This broader region, influenced by the indistinct and narrow PF, was found to exhibit the highest biological activity and biogeochemical changes. Therefore, we gave this wider region a special name: Polar Frontal region (PFr). This term should not be confused with the existing definition of the Polar Frontal Zone (see above). The region to the south of the PFr is termed the southern ACC zone (sACC) and covers the area between the southern edge of the PFr (at about 50°S) and the northern rim of the Weddell Gyre. The transition between the PFr and the sACC was marked by a sharp decline in chlorophyll concentrations and a slight increase in salinity (Bathmann *et al.*, 1997). The sF—located at ~56°S and clearly recognisable in the dynamic topography (Veth *et al.*, 1997)—is included here within the overall southern ACC complex.

The AWB is also a front that constitutes the southern boundary of the ACC, and hence is part of the overall ACC system. During the *Polarstern* cruise ANT X/6, it was located between 57° and 58°30′S, with the frontal jet near 58°S (Veth *et al.*, 1997). Although the salinity of Weddell Gyre surface water is much higher than that of the sACC, the transition between the water masses in the surface layer was obscured during the cruise by the dilution

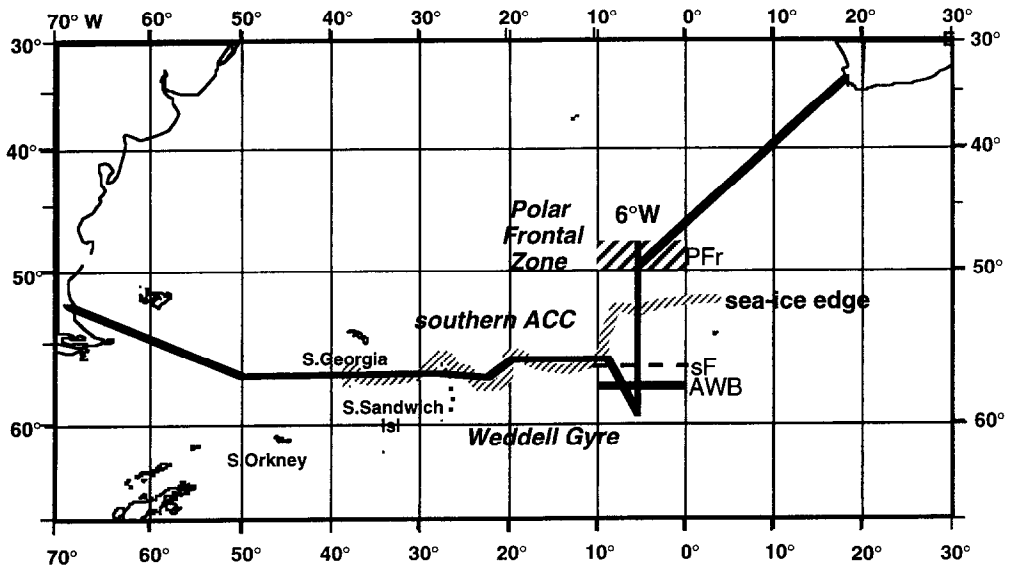

Fig. 1. The cruise track of expedition ANT X/6 from 29 September to 29 November 1992 (modified from Bathmann *et al.*, 1997). Most work was done in a series of sections along the 6°W meridian. Also shown are the typical positions of the fronts between more extensive and homogeneous zones: Polar Frontal Zone or northern branch of the Antarctic Circumpolar Current (ACC), Polar Front (PF), southern ACC branch (sACC) with southern Front (sF) and ACC–Weddell Gyre Boundary (AWB); Weddell Gyre. The ice edge, shown as originally encountered in early October, had shifted south to the AWB by the middle of November.

effects of meltwater and the absence of any clear signal in plankton concentrations (Bathmann *et al.*, 1997).

The marginal ice zone (MIZ) is determined by the edge of the ice cover, which retreated by about 400 km from 54°30′ to ~ 58° S during the period of our cruise. The MIZ comprises the transition from closed, but melting, pack ice, through the zone of dispersing ice floes and into open, completely ice-free waters under the influence of melt water. The ice cover is strongly influenced by wind drift, leading to a highly irregular, meandering ice edge (see satellite image in Veth *et al.*, 1997).

CRUISE DESCRIPTION

The R.V. *Polarstern* sailed from Punta Arenas, Chile, on 29 September 1992 with 51 scientists representing five European countries (Belgium, Denmark, France, Germany and The Netherlands). The west–east transect (Transect 1, Fig. 1), at first carried out along the 57°S parallel and later shifted north to 56°S, began at 49°W on 2 October and terminated at 6°W on 12 October. A station was conducted each day at which various gear, including the CTD rosette and nets, were deployed. Chlorophyll fluorescence together with salinity and temperature were recorded continuously in water pumped from the bow of the ship (8 m depth) throughout the cruise (Bathmann *et al.*, 1997). The tracks of surface recordings have been assigned transect numbers as indicated in Fig. 2. A list of all stations occupied is provided in Table 2.

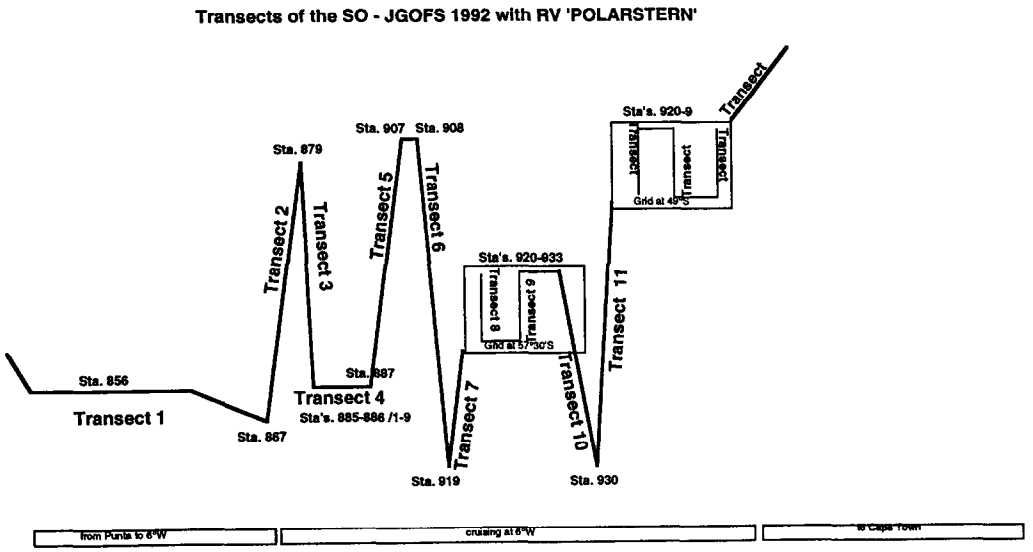

Fig. 2. The transects numbered 1–13 of the ANT X/6 expedition. Most north/south transects were positioned along the 6°W meridian and provided a series of sections of the ACC with ongoing spring season.

The 57°S parallel was chosen as the cruise track in the western section of Transect 1 as it crossed from open ACC water not influenced by ice, across the marginal ice zone (MIZ) of the Weddell–Scotia Confluence (WSC), and into closed pack ice encountered at 20°W. The transect passed through the arc of the South Sandwich islands at about 26°W. Heavy pack ice at 20°W slowed progress, so the track was shifted north to open water along 56°S. This eastern section of Transect 1 again crossed from open sACC water, through the MIZ and into closed ice pack of the Weddell Gyre at 6°W (Fig. 1).

On the basis of topography and ice cover, the 6°W meridian was chosen as the study site. The bottom topography here is less complicated than in the vicinity of the Greenwich Meridian where the mid-Atlantic Ridge meets the America–Antarctic Ridge. On 13 October the first station (868) of Transect 2 was conducted deep in closed pack ice. Thereafter, stations were conducted at 30 nautical mile intervals northward until Sta. 876 was made at 53°00′S on 15 October; the transect had to be interrupted after this station because of a storm and the next station was carried out when calmer waters were reached in the PFr at 49°S (Sta. 877) on 17 October. Transect 2 was continued until Sta. 879 at 48°S on 18 October. From there we commenced Transect 3 on our way south along 6°W, sampling stations at 49°30′S, 50°00′S and 50°30′S; the last station had to be interrupted again because of a storm. A station gap between 51° and 53°S was enforced on these two first south–north–south transects (2 and 3).

On our return to the ice edge after 10 days, the pack-ice edge had dispersed significantly and a 100-km-wide, loose ice field extended northward, peninsula-like in the study area (satellite photograph in Veth *et al.*, 1997). We carried out a drift station, termed Transect 4, in this marginal ice zone within the ice peninsula at about 56°S and 7°W. The drifter carried a sediment trap and *in situ* incubation bottles. The rationale for site selection was the expected presence of a shallow melt-water layer subjected to an adequate light supply within

Table 2. List of all stations during ANT X/6; trans: west–east section

Station	Date	Latitude	Longitude	Region	Station	Date	Latitude	Longitude	Region
856	2.10.92	56° 46.1 S	50° 00.1 W	trans	905	29.10.92	48° 00.0 S	06° 00.0 W	PFr
857	2.10.92	56° 51.8 S	49° 35.4 W	trans	906	30.10.92	47° 29.9 S	05° 59.9 W	PFr
858	3.10.92	57° 00.1 S	45° 13.8 W	trans	907	30.10.92	46° 59.8 S	06° 00.0 W	PFr
859	4.10.92	56° 59.9 S	38° 51.3 W	trans	908	30.10.92	46° 52.3 S	05° 43.0 W	PFr
860	5.10.92	56° 59.4 S	30° 26.5 W	trans	909	2.11.92	55° 00.1 S	06° 00.6 W	sACC
861	6.10.92	56° 58.3 S	29° 12.8 W	trans	910	2.11.92	55° 29.9 S	05° 59.8 W	sACC
862	7.10.92	56° 59.6 S	23° 18.5 W	trans	911	3.11.92	55° 51.0 S	05° 59.6 W	sACC
863	8.10.92	56° 51.0 S	21° 20.5 W	trans	912	3.11.92	56° 01.1 S	06° 00.8 W	sACC
864	9.10.92	56° 09.1 S	15° 25.5 W	trans	913	3.11.92	56° 30.1 S	06° 00.2 W	sACC
865	9.10.92	56° 09.1 S	15° 25.5 W	trans	914	4.11.92	57° 00.2 S	05° 59.6 W	sACC
865a	10.10.92	56° 03.0 S	09° 32.6 W	trans	915	4.11.92	57° 29.4 S	06° 00.4 W	MIZ
866	11.10.92	57° 44.7 S	06° 28.6 W	trans	916	4.11.92	57° 59.8 S	05° 59.7 W	MIZ
867	12.10.92	57° 18.3 S	06° 12.5 W	trans	917	5.11.92	58° 29.2 S	05° 59.9 W	MIZ
868	12.10.92	56° 59.6 S	06° 00.4 W	trans	918	6.11.92	59° 00.2 S	06° 00.2 W	MIZ
869	13.10.92	56° 30.8 S	05° 59.3 W	trans	919	6.11.92	59° 29.4 S	05° 59.8 W	MIZ
870	13.10.92	55° 59.9 S	05° 59.8 W	MIZ	920	7.11.92	57° 15.1 S	05° 58.6 W	MIZ
871	14.10.92	55° 28.4 S	05° 57.6 W	MIZ	921	8.11.92	57° 30.0 S	06° 01.5 W	MIZ
872	14.10.92	55° 00.1 S	06° 02.8 W	MIZ	922	8.11.92	57° 45.2 S	06° 00.7 W	MIZ
873	14.10.92	54° 29.7 S	06° 00.3 W	MIZ	923	8.11.92	58° 00.0 S	06° 00.2 W	MIZ
874	15.10.92	53° 59.9 S	05° 59.8 W	sACC	924	8.11.92	58° 00.0 S	06° 30.6 W	MIZ
875	15.10.92	53° 30.0 S	06° 00.0 W	sACC	925	8.11.92	57° 45.6 S	06° 30.1 W	MIZ
876	15.10.92	53° 00.1 S	05° 59.9 W	sACC	926	8.11.92	57° 29.8 S	06° 30.7 W	MIZ
877	17.10.92	49° 00.3 S	06° 00.1 W	PFr	927	9.11.92	57° 15.1 S	06° 29.8 W	MIZ
878	18.10.92	48° 30.3 S	06° 00.2 W	PFr	928	9.11.92	57° 00.0 S	06° 30.3 W	MIZ
879	18.10.92	48° 00.1 S	06° 00.1 W	PFr	929	10.11.92	59° 00.1 S	06° 16.3 W	MIZ
880	19.10.92	48° 49.4 S	05° 59.5 W	PFr	930	10.11.92	59° 30.1 S	06° 00.2 W	MIZ
881	19.10.92	49° 30.2 S	05° 59.5 W	PFr	931	10.11.92	58° 59.8 S	05° 59.5 W	MIZ
882	19.10.92	49° 59.5 S	05° 59.8 W	PFr	932	11.11.92	58° 29.8 S	05° 59.5 W	MIZ
883	20.10.92	50° 29.8 S	05° 59.8 W	sACC	933	11.11.92	58° 13.2 S	05° 59.1 W	MIZ
884	21.10.92	54° 16.9 S	06° 17.3 W	sACC	934	11.11.92	57° 59.7 S	06° 00.5 W	MIZ
885	22.10.92	55° 53.7 S	06° 59.9 W	MIZ	935	12.11.92	57° 58.8 S	05° 53.4 W	MIZ
886	22.10.92	56° 04.3 S	06° 50.6 W	MIZ	936	12.11.92	57° 59.1 S	06° 00.7 W	MIZ
887	24.10.92	55° 59.3 S	06° 03.7 W	MIZ	937	12.11.92	57° 51.9 S	05° 59.9 W	sACC
888	24.10.92	55° 45.0 S	06° 00.1 W	MIZ	938	12.11.92	57° 44.7 S	06° 00.5 W	sACC
889	24.10.92	55° 30.0 S	05° 59.8 W	sACC	939	12.11.92	57° 29.7 S	06° 00.0 W	sACC
890	25.10.92	55° 15.1 S	06° 00.0 W	sACC	940	12.11.92	57° 14.9 S	06° 00.1 W	sACC
891	25.10.92	55° 00.5 S	06° 00.3 W	sACC	941	12.11.92	57° 03.3 S	06° 00.5 W	sACC
892	26.10.92	54° 30.3 S	05° 59.7 W	sACC	942	13.11.92	56° 30.1 S	06° 00.0 W	sACC
893	26.10.92	54° 00.0 S	06° 00.7 W	sACC	943	13.11.92	56° 00.5 S	06° 00.1 W	sACC
894	26.10.92	53° 30.1 S	06° 00.1 W	sACC	944	14.11.92	55° 30.0 S	05° 59.9 W	sACC
895	26.10.92	53° 00.0 S	05° 59.7 W	sACC	945	14.11.92	55° 00.2 S	06° 00.8 W	sACC
896	27.10.92	52° 30.2 S	06° 00.1 W	sACC	946	14.11.92	54° 30.0 S	05° 59.9 W	sACC
897	27.10.92	52° 00.2 S	06° 00.0 W	sACC	947	15.11.92	53° 59.8 S	06° 00.2 W	sACC
898	27.10.92	51° 30.2 S	06° 00.3 W	sACC	948	16.11.92	52° 59.9 S	05° 59.5 W	sACC
899	27.10.92	50° 59.9 S	06° 00.0 W	sACC	949	16.11.92	52° 59.9 S	05° 59.5 W	sACC
900	28.10.92	50° 30.1 S	05° 59.8 W	sACC	950	16.11.92	52° 29.7 S	06° 00.2 W	sACC
901	28.10.92	50° 00.1 S	05° 59.6 W	PFr	951	16.11.92	52° 00.0 S	06° 00.0 W	sACC
902	28.10.92	49° 30.0 S	06° 00.1 W	PFr	952	17.11.92	51° 29.9 S	06° 00.5 W	sACC
903	29.10.92	49° 00.0 S	06° 00.1 W	PFr	953	17.11.92	50° 59.7 S	06° 00.6 W	sACC
904	29.10.92	48° 30.5 S	06° 00.1 W	PFr	954	17.11.92	50° 30.0 S	06° 00.0 W	sACC

(*Continued*)

Table 2. Continued

Station	Date	Latitude	Longitude	Region
955	18.11.92	50° 15.0 S	06° 00.1 W	sACC
956	18.11.92	49° 59.0 S	06° 00.2 W	PFr
957	18.11.92	49° 44.9 S	05° 59.7 W	PFr
958	18.11.92	49° 30.0 S	06° 00.0 W	PFr
959	19.11.92	49° 15.0 S	05° 59.8 W	PFr
960	19.11.92	49° 00.0 S	05° 59.9 W	PFr
961	19.11.92	48° 44.8 S	05° 59.1 W	PFr
962	19.11.92	48° 30.2 S	05° 59.8 W	PFr
963	19.11.92	48° 15.1 S	06° 00.0 W	PFr
964	20.11.92	48° 00.1 S	06° 00.1 W	PFr
965	20.11.92	47° 44.8 S	05° 59.9 W	PFr
966	20.11.92	47° 30.0 S	06° 01.0 W	PFr
967	20.11.92	47° 46.1 S	06° 11.4 W	PFr
968	20.11.92	47° 14.9 S	06° 00.0 W	PFr
969	21.11.92	46° 59.5 S	06° 00.1 W	PFr
970	21.11.92	48° 00.1 S	05° 59.9 W	PFr
971	21.11.92	48° 15.2 S	06° 00.3 W	PFr
972	22.11.92	48° 30.1 S	06° 00.2 W	PFr
973	23.11.92	49° 00.2 S	06° 00.0 W	PFr
974	23.11.92	49° 14.9 S	05° 59.7 W	PFr
975	23.11.92	49°30.0 S	06° 00.0 W	PFr
976	23.11.92	49°45.0 S	06° 00.0 W	PFr
977	23.11.92	50°00.2 S	06° 00.0 W	PFr
978	23.11.92	49°45.0 S	06° 00.0 W	PFr
979	25.11.92	45°29.7 S	01° 08.2 E	PFr

this dispersed ice field. Because none of the floes was large enough to serve as a buoy, the drifter was deployed in a broad band of open water between fields of crushed ice. We found it very difficult to keep track of the drifter as it was engulfed frequently in ice fields that, because they were wind-driven, moved much faster than the underlying water mass. In addition, biomass was very low and horizontal heterogeneity in water column structure was found during the drift. Wind speeds increased considerably after 2 days, so the drifter had to be recovered on 24 October. Nevertheless, two 24-h *in situ* incubations, one sediment trap collection and a series of water column measurements were obtained in this period. The sediment trap collected a negligible amount of material and these results have not been considered.

South–north Transect 5 began on 24 October at 56°S and 6°W (Sta. 887) and ended successfully without interruption on 30 October at 47°S (Sta. 907) in the PFr. Chlorophyll concentrations had increased significantly at the PFr but were at much the same low levels in the MIZ as in the open sACC. After a deep station at 46°52′S and 5°43′W, *Polarstern* returned south to the ice edge (Transect 6). The next plan was to carry out a detailed section (southern part of Transect 6) with stations at 30 nautical mile (55.6 km) intervals from open water, deep into closed pack ice. The rationale for this short detailed transect was to obtain better spatial coverage of the situation at the MIZ than had been achieved with the drifter. The first station of this short section was taken on 2 November at 55°00′S (Sta. 909) and the last (Sta. 919) at 59°30′S on 6 November in pack ice cover that was breaking up and melting. This detailed evaluation of the broad, melting ice edge indicated that accumulation of phytoplankton biomass was not occurring in the region, although melt-water layers—albeit not strongly stratified—were indeed present. The residence time of these shallower layers may not have been long enough to enable significant build-up of biomass, possibly because of the frequent storms which crossed this latitudinal zone and resulted in regular deep mixing of the water column. In contrast, the PFr experienced comparatively low wind speeds throughout the investigation because of a stable high pressure area in the PFr.

Surface temperature recordings indicated the persistent presence of a band of warmer water at the ACC–Weddell Gyre boundary at *ca* 58°S. As this could only be explained by upwelling of warm Circumpolar Deep Water and a corresponding downwelling of denser

Weddell Gyre surface water, a closer examination of the phenomenon was called for as it affected surface-layer dynamics and hence biomass accumulation. Accordingly, we carried out a grid of CTD-stations (920–928 and Transects 7–10) across the front which was interrupted by a brief but intense storm. The upwelling of warm water along 58°S appeared as a "nose" in temperature profiles of Stas 934–937 that moved up the water column. The "nose" was still evident at 40 m depth in Sta. 937. This process, not dealt with in any of the papers of this issue, would have resulted in disruption of the surface layer and dilution by deep, plankton-poor water along the front.

The final major transect (11) from south-to-north began on 10 November at 59°30′S. The southernmost station was located at the edge of an extensive, intact ice floe, deep in closed pack ice. The transect was completed successfully with stations at 30 nautical mile (55.6 km) intervals on 21 November at 47°00′S. On 20 November a detailed study of the surface water around a large iceberg was conducted from an inflatable boat to record trace metal concentrations in its vicinity and to relate these to melt-water plumes emanating from it.

Phytoplankton biomass had increased significantly in the PFr, and three distinct blooms were found, each characterised by the dominance of different diatom species (*Fragilariopsis kerguelensis*, *Corethron inerme* and *C. criophilum*). It was decided to use the remaining time to sample these blooms in detail. Stations were conducted at 15 nautical mile intervals from 48°00′ to 50°00′S (Transect 12 and Stas 970–977) with more detailed stations at the sites of biomass peaks (Stas 972 and 978). The transect was completed on the night of 23/24 November after which R.V. *Polarstern* steamed to Cape Town with underway measurements of chlorophyll (Chl) *a* and bird abundance (Transect 13). The cruise ended on 30 November 1992.

MAJOR FINDINGS OF THE CRUISE

The results obtained during the cruise, presented in detail in the separate papers of this issue, are summarised briefly. A major finding was the negligible build-up of plankton biomass and concomitant absence of CO_2 drawdown in association with seasonal retreat of the ice cover. In striking contrast to this unexpected poverty of both the MIZ and the frontal region of the AWB, large phytoplankton blooms, dominated by different diatom species, accumulated in the PFr. As expected, chlorophyll stocks in the sACC remained monotonously low throughout the study. The authors of this issue have therefore, by and large, placed more emphasis on observations from the PFr compared to the MIZ despite the much better coverage achieved by the 11 transects (including the drift station) that crossed the retreating ice edge.

It should be pointed out here that three to five CTD-casts, necessitated by the inordinate demands for water onboard, were carried out at each of the major stations; the casts were interspersed by deployment of various other gear, and the stations lasted 5–8 h. Because of the effects of small-scale heterogeneity, particularly in the PFr (Bathmann *et al.*, 1997), results from different CTD casts at the same station sometimes differed substantially. This problem was overcome by avoiding direct comparisons of data from different casts. Each cast sampled the entire surface layers and, where relevant, chlorophyll concentrations were measured at each depth to ensure that the various casts were independent. Intercalibration of the methods used for measuring chlorophyll on board yielded very similar results. Thus, although somewhat different chlorophyll values are reported from the same stations in the PFr in papers dealing with productivity, phytoplankton biomass and species composition,

pigments and biogenic silica distributions (Jochem *et al.*, 1995; Quéguiner *et al.*, 1997; Bathmann *et al.*, 1997; Peeken, 1997, respectively), the main findings are not affected by the discrepancy.

A comparison of the data collected during the three north–south sections clearly reflected a seasonal trend particularly evident in the blooms in the PFr. Relating the observed changes between transects quantitatively to one another is justified by the zonal position maintained by the eastward flowing water masses studied. Indeed, the position of the southern fronts hardly changed between transects. In contrast, the Polar Front meandered considerably, resulting in latitudinal displacement of biomass peaks between transects. The continuous surface recordings ensured that no major features were overlooked between the stations and the species composition of the plankton enabled tracking of the blooms. The procedure used to quantify seasonal changes in properties of the water masses has been described by de Baar *et al.* (1995). The production of new organic material in the surface water during the bloom, the subsequent export to deeper layers, as well as the decomposition of organic matter at greater depths leaves traces on a variety of time scales that are exploited for quantification. The time scales range from about a year (nutrients) through several months (air–sea equilibria of CO_2), 1 month (half-life of ^{234}Th), to weeks (composition of the plankton).

The physical conditions

The CTD profiles from the various north/south transects over the 6-week period of study have been presented and discussed by Veth *et al.* (1997). The data reveal a strong variability in the PFr indicating meandering and eddy-shedding. In striking contrast, the two frontal systems crossed by the retreating ice edge—the sF and the AWB—remained remarkably stable. Veth *et al.* (1997) suggest that the differences in hydrography between the PFr and the two southern fronts are due to bottom topography. Whereas the America–Antarctic Ridge constrains the position of the two southern fronts, no such feature underlies the Polar Front at 6°W.

Because of meandering of the PF, its zone of influence—the PFr—was much broader than in the case of the stable fronts. This can be seen from the more complex structure reflected in isopycnals in the upper 100 m of the PFr as compared to corresponding isopycnals in the southern fronts. The stability of the water column was greater in the PFr, particularly during Transect 11, than in the south (Jochem *et al.*, 1995). The blooms that developed in the PFr were closely related to hydrographical features of the upper layer although high chlorophyll values (> 0.5 Chl a m^{-3}) extended to about 100 m depth. Hence vertical biomass distribution did not simply mirror the density field.

The deepest mixed layers occurred throughout the sACC, but distinctly shallower in a narrow band—evident in all the transects—along the AWB. The AWB was covered by ice during most of the study period and the ice edge coincided with the AWB at the time Transect 11 was carried out. The highest chlorophyll values recorded in the MIZ during this study (> 0.4 Chl a m^{-3}) were located in the narrow band associated with the AWB after retreat of the ice cover. Although the ice cover retreated from 55°S to 58°S between Transects 2 and 11, the only significant increase in chlorophyll concentrations observed in its wake were associated with the AWB. Zones influenced by melt-water were evident in the continuous surface recordings of salinity but these had no noticeable effect on chlorophyll values measured concomitantly (Bathmann *et al.*, 1997).

Diatom blooms in the Polar Frontal region

Three distinct phytoplankton blooms which extended below 70 m depth, each dominated by a different diatom species (*Fragilariopsis kerguelensis*, *Corethron inerme* and *C. criophilum*), developed during the 6 weeks of investigation in the PFr. Peak chlorophyll values increased from 0.7 mg Chl *a* m^{-3} in Transects 2/3 to >4 mg Chl *a* m^{-3} in Transect 11/12 (Bathmann *et al.*, 1997). The peak standing stocks attained by the PFr blooms were 177, 223 and 277 mg Chl *a* m^{-2}, respectively. These are large stocks by open ocean standards, as are the primary production rates of up to 3 g C m^{-2} day^{-1} recorded here (Jochem *et al.*, 1995). Nutrient and chlorophyll concentrations were closely correlated. However, because of the deep extension of the bloom, nitrate and phosphate depletion amounted to only about a third of the concentrations present in low-chlorophyll winter water below the bloom. Silicate depletion was more substantial (approximately two-thirds), and the lowest values recorded were 8.4 μM.

The role of diatoms in development of the bloom is shown by Quéguiner *et al.* (1997) who studied the distribution of biogenic silica (BSi). Whereas the BSi/POC molar ratio in the sACC as well as near the ice edge remained low (0–200 m averages 0.04–0.13), this ratio increased to a maximum of 1.75 in the *Fragilariopsis* bloom, confirming the presence of heavily silicified diatoms. This high ratio, the occurrence of a BSi maximum at depth, and the abundance of empty diatom frustules all point to the potential for a large export of biogenic silica in the PFr.

An effective mechanism for selective export of Si relative to organic matter was found in the *Corethron criophilum* bloom where a large part of the population had entered the sexual phase (Crawford, 1995). Discarded gametangial cell walls were found throughout the water column, and their abundance at depths of several 100 m indicated that they were sinking out faster than the living cells in the bloom. Such sexual events can be triggered in cells of this species when, in the course of size-reducing, vegetative division, they attain a specific diameter. The organic matter of male gametangia is converted into sperm that swim out of the cell wall, thus effectively entering the nanoflagellate population. The original cell wall of the female gametangium is also discarded during auxospore formation. Crawford and Hinz (1997) have analysed size spectra of *Corethron* populations in the PFr and demonstrated gaps at certain size classes presumably due to formation of gametangia.

Carbon dioxide

The uptake of CO_2 is clearly visible in the distribution of pCO_2 which decreases with the development of the bloom (Bakker *et al.*, 1997). The authors show that the resulting influx from the atmosphere during the period of the cruise is small, but that the CO_2 uptake by phytoplankton is masked by the temperature increase, which reduces the CO_2 solubility. The actual CO_2 fixation in the PFr was about twice as high as expected from the drop in pCO_2 alone. Such biologically driven CO_2 uptake in combination with the local formation of Antarctic Intermediate Water would lead to drawdown of CO_2 in the relatively narrow region of the Polar Front. However, in the vast region of the southern ACC, the seasonal warming effect during spring would yield an overall release of CO_2 to the atmosphere. In the sF as well as the AWB where sea-ice had recently melted, an even larger release of CO_2 from sea to air appears to be the result of the contact with the atmosphere of water masses oversaturated in CO_2 due to upwelling and wintertime mineralisation. Overall, the distinct

sink function at the PFr combined with significant source functions in the sACC, sF and AWB yields an overall minor sink function for CO_2 from air to sea for the spring period of observations over the whole section (Bakker *et al.*, 1997).

The incorporation of dissolved $CO_{2(aq)}$ into plankton biomass is accompanied by fractionation of the stable isotope ^{13}C versus the common isotope ^{12}C. At higher concentrations of $CO_{2(aq)}$ in seawater this fractionation is more pronounced and the ensuing isotopic ratio $^{13}C/^{12}C$ of particulate organic carbon (POC) generally lower. An inverse relationship between $CO_{2(aq)}$ and $^{13}C/^{12}C$ of POC appears to exist in surface waters of the world ocean, which has led to the suggestion that the paleo-CO_2 contents of surface waters can be deduced from $^{13}C/^{12}C$ in paleo-organic matter. However, variations of $^{13}C/^{12}C$ in POC observed in the sACC and PFr (Dehairs *et al.*, 1997a) cannot be explained satisfactorily by ambient $CO_{2(aq)}$ and growth rate as the only factors controlling $^{13}C/^{12}C$ of phytoplankton. The authors suggest a relative shift from Calvin cycle carboxylation to b-carboxylation, possibly due to changes in nitrogen nutrient supply. Obviously the prospects for reconstruction of paleo-CO_2 values are complicated by the intricacies of plant physiology.

Iron and the diatom blooms

Dissolved iron (Fe) was found at sub-nanomolar (<1 nM $= 10^{-9}$ mol dm^{-3}) concentrations in surface waters over most of the ACC (de Baar *et al.*, 1995; Löscher *et al.*, 1997). Basin-wide upwelling appears to maintain these low levels of dissolved iron, adequate for sustenance of the characteristic microbial foodweb operating at constantly low biomass levels in surface waters (de Baar *et al.*, 1995). Unexpected higher concentrations of dissolved Fe averaging at 1.87 nM (section 5/6) and 1.14 nM (section 11) were found in the PFr (de Baar *et al.*, 1995). Their coincidence with the diatom blooms and CO_2 undersaturations provides evidence for the hypothesis of Martin *et al.* (1990) that iron availability through the agency of phytoplankton blooms is crucial for drawdown of atmospheric CO_2 in HNLC areas (de Baar *et al.*, 1995). However, as mentioned above, water column stability at the PFr was also more conducive to bloom development than in the sACC.

The underlying threshold-effect of iron for plankton growth rates at adequate light levels was established by shipboard iron-enrichment experiments that also provided further insight into iron regulation of the phytoplankton community (van Leeuwe *et al.*, 1997; Scharek *et al.*, 1997). In five incubation series, the addition of iron always led to enhanced synthesis of Chl *a* and nutrient uptake. Remarkably, the response was weaker for experiments starting with low initial biomass in the sACC, and stronger for those starting with higher initial biomass of diatoms in the PFr (Scharek *et al.*, 1997). Possibly the dominant diatom species encountered (*Fragilariopsis kerguelensis* and *Corethron* spp.) in the PFr have a higher cellular Fe requirement, but they also may be capable of assimilating Fe more rapidly. The latter hypothesis would fit the observations, but needs verification by controlled laboratory experiments of the individual species. The communities in the shipboard experiments responded to iron enrichment largely by increasing the overall rate of growth (reflected in, for example, e.g. assimilation rates of $H^{14}CO_3$, $^{15}NO_3$, ^{14}C incorporation in organic pools and lower C/N ratios), with two notable exceptions. The synthesis of Chl *a* was more strongly enhanced, whereas uptake of phosphate was less affected in comparison to overall growth rates. The latter observations of the modest role of

Fe in phosphate uptake versus, among others, nitrate uptake was consistent with field observations of increasingly high nitrate/phosphate ratios in waters where blooms of *Fragilariopsis kerguelensis* had developed (de Baar *et al.*, 1997).

The distribution of particulate Al showed maxima in surface waters coinciding with the same hydrographic fronts where dissolved Fe also was somewhat (AWB) or much (PFr) higher (Löscher *et al.*, 1997). This hints at rapid eastward transport of water masses within the AWB and PFr bearing Al and Fe, both originating from terrigenous sources. Hence the higher dissolved Fe in the PFr could have been derived from terrigenous sources as well. If this is the source of higher iron, then the 6°W section, or at least the AWB (~56–58°S) and the PFr (~48–50°S), were not as land-remote as we had hoped. This appears to be confirmed by lower dissolved Fe observed at AWB and PFr in a study conducted further to the east at 6–12°E in summer of 1995/96 (de Baar *et al.*, unpublished data). Another potential source of iron was the unusually high iceberg concentration of 5–15 bergs/100 km^2 found throughout the PFr on all transects by visual observations of J. van Franeker (Bathmann *et al.*, 1994). None was observed in the PFZ during the 1995/1996 study mentioned above. Significantly higher iron concentrations than background values were found by us in the melt-water wake of the iceberg. However, calculation of melt-water input from icebergs based on the slightly lower salinity of the PFr indicates the contribution to have been trivial (de Baar *et al.*, 1995). It cannot yet be decided whether the source of Fe and Al for surface waters is in the continental margins (i.e. Antarctic Peninsula and South American shelf) or is related to the aeolian input of continental dust from South America, most notably at the PFr and Polar Frontal Zone (Kumar *et al.*, 1995).

Microbial food web

Flow cytometry showed that autotrophic pico- and nanoplankton contributed up to 90% of total chlorophyll *a* in regions of low chlorophyll concentrations, but less than 50% in the PFr where phytoplankton biomass accumulated (Detmer and Bathmann, 1997). Hence, the populations of these small primary producers, albeit subject to moderate fluctuations, represent a ubiquitous, stable component of surface waters. The build-up of phytoplankton blooms in the PFr was due to the large diatoms. This was also confirmed by pigment distributions measured by HPLC (Peeken, 1997). These data showed that, besides the dominating diatoms, prymnesiophytes, autotrophic dinoflagellates, cryptophytes and prasinophytes were present. A significant contribution of chlorophytes to total biomass of nanophytoplankton also was reported. The low-chlorophyll areas differed in the relative contributions of the algal groups listed above. Thus, the species composition in what appeared to be a homogeneous environment must have differed considerably.

Bacterial standing stock and growth broadly followed the patterns of phytoplankton development, exhibiting highest values in the PFr during the last transects when phytoplankton had attained the highest biomass (Lochte *et al.*, 1997). However, bacteria consumed less than 30% of primary production at the PFr and MIZ but an average of 66% in the sACC. This indicates that bacterial development may lag behind that of phytoplankton or may become uncoupled during bloom development.

Dissolved organic carbon (DOC) showed constant concentrations of presumably quite refractory substances in deep waters (Kähler *et al.*, 1997). Elevated DOC concentrations in surface waters, expected from phytoplankton exudation, were seldom observed and showed no relation to hydrographic features. These observations point to the highly labile nature of

this excess DOC in surface waters, which was confirmed by the rapid bacterial consumption of natural DOC in experiments.

Nanoprotozoa are increasingly recognized as important grazers of small phytoplankton cells and microbes. On average, nanoprotozoan biomass was equivalent to 77% of the biomass of potential prey, namely bacteria and phototrophic flagellates (Becquevort, 1997). Very high ingestion rates were found in experiments for dinoflagellates, this being the dominant nanoprotozoan group, implying a high grazing impact on nanophytoplankton. Consumption of daily production of bacterioplankton and small phytoplankton by nanoprotozoa was estimated to range from 32 to 40%. Hence these small consumers are able to exert a heavy grazing pressure on the components of the microbial loop. They may be responsible for suppressing biomass accumulation within the microbial network.

Some classes of phytoplankton produce significant amounts of the osmolyte dimethylsulphoniopropionate (DMSP), the precursor of dimethyl sulphide (DMS). The latter may escape into the atmosphere and, following conversion to sulphate, eventually serve as condensation nuclei for cloud formation, thus affecting climate. Most previous studies of the Antarctic region have focused on DMS in nearshore areas and ice edge blooms where high fluxes from sea to air sometimes were reported. Based on these results the Southern Ocean is widely considered a major source of DMS to the atmosphere. Meyerdierks *et al.* (1997) could not confirm this view as they found fairly low concentrations of DMSP in the open waters of the sACC. The slightly higher values in the PFr were largely confined to the 5–20-μm size classes, there being very little DMSP in the diatom-dominated >20-μm size fraction.

Zooplankton grazing

The larger protozooplankton, including heterotrophic dinoflagellates, ciliates, radiolarians and foraminifers, are known to feed on particles >20 μm and therefore diatoms. The composition of this group showed clear regional differences although total biomass across the sACC and PFr was roughly similar and averaged about 300 mg C m^{-2}. Standing stocks were distinctly lower in the MIZ. Grazing pressure exerted by this group in the sACC and PFr ranged between 10 and 33% of daily primary production and was only 7% in the MIZ (Klaas, 1997). The contribution of radiolarians and foraminifers to total protozoan biomass was negligible (Klaas, 1996).

Copepods were the dominant metazooplankton in the PFr and the AWB; among the copepods the group of cyclopoids was the most numerous and was found to occur at rather shallow depths in the PFr (Fransz and Gonzalez, 1997). In contrast, copepod abundance was low in the open waters of the sACC. In all regions, the grazing impact of the various copepod species was found to be quite modest, in the PFr accounting for consumption of only about 1% of the carbon fixed in primary production (Dubischar and Bathmann, 1997). Salps were quite abundant in the oligotrophic waters of the sACC. Salps filter large volumes of water per day, but not enough is known to assess their grazing impact on pelagic systems. Salp ingestion rates estimated on board indicate that the salp population in the sACC may well be capable of consuming the entire primary production, thus preventing the accumulation of algal biomass (Dubischar and Bathmann, 1997). Further, salp grazing should have a negative effect on other zooplankters including copepods.

Export production

Although the build-up of organic material, as well as the uptake of nutrients and CO_2, had already been observed during Transect 5, significant particle export did not occur until after this transect. A depletion of total ^{234}Th (24.1 day half-life) with respect to dissolved parent ^{234}U did not develop before the penultimate Transect 11 (Rutgers van der Loeff *et al.*, 1997). The authors use this depletion to calculate the export production of organic carbon. Friedrich (1996) shows the corresponding results for the isotopes ^{210}Po and ^{210}Pb (included in a database). As a result of their longer residence times of 138 days and 22.3 years, respectively, the distributions of these isotopes are affected by lateral advection to a greater degree than that of ^{234}Th. The tracers have widely different adsorption behaviour, and consequently trace different particle classes. Polonium-210 appears to be more suitable as a tracer for POC flux, whereas ^{210}Pb may be a more suitable tracer for biogenic silica flux.

Mineralisation at depth results in the consumption of oxygen and in the precipitation of microcrystals of barite. Indeed, a maximum concentration of particulate barite was found at depths of several hundred meters coincident with the maximum in oxygen utilization rate, which was derived from an inverse one-dimensional diffusion–advection–consumption model (Dehairs *et al.*, 1997b). Part of the mesopelagic barium stock is formed by mineralisation activity during the bloom, whereas another part of the stock seems to have a longer time scale and rather represents a signal accumulated over various seasons.

Top predators

Another transfer route for organic production is by the respiration and biomass build-up of birds and mammals. Abundances of top predators were quite low in the open waters and significantly higher at and around the MIZ (van Franeker *et al.*, 1997). In all regions the CO_2 respiration by air-breathing organisms, calculated on the basis of their abundance and general metabolic relationships, was found to be negligible, at most 0.3–0.6% of the CO_2 fixation in open-water primary production. Nevertheless, top predators may have an effect on the pelagic system and biogeochemical cycling by influencing the population dynamics of their prey, these largely being the organisms in the size range down to mesozooplankton, i.e. salps, krill and copepods.

DISCUSSION AND CONCLUSIONS

The constantly low chlorophyll concentrations recorded over the major part of the study area during 6 weeks indicate that growth and loss rates in the water column were balanced. The growth rate of the phytoplankton stock was apparently suppressed by a combination of deep mixing and low iron availability. Loss rates will have been primarily due to grazing (by salps and protozoa) as $^{234}Th/^{234}U$ ratios indicated that sinking was a minor factor. Hence, the plankton of these areas, dominated by nanoflagellates, can be classified as regenerating communities with little impact on biogeochemical fluxes (Smetacek *et al.*, 1990). In contrast, diatom biomass increased successively during the investigation period in the PFr. Obviously, growth conditions were more favourable in the PFr, and it is reasonable to assume that phytoplankton in all size classes will have responded by increasing their growth rates. However, only the larger diatoms accumulated, suggesting that they are subject to lower grazing pressure than the nanoflagellates comprising the regenerating system.

However, grazing pressure on the larger phytoplankton was lowest in the MIZ, yet diatom biomass did not increase there. The results of our cruise, discussed in the following sections suggest that phytoplankton blooms are induced by combinations of factors.

Physical conditions

The results of this cruise support the emerging view that frontal systems play a prominent role in regulating productivity and hence the rates of biogeochemical processes in the Southern Ocean (Lütjeharms *et al.*, 1985; Bianchi *et al.*, 1992; Laubscher *et al.*, 1993; Turner and Owens, 1995). A comparison between the ecological conditions prevailing in the PFr with those in the adjoining sACC clearly illustrates why blooms developed only in the former region. The monotonously low biomass levels of the sACC were apparently maintained by the combination of low growth rates (deep mixing and lower iron availability) and high grazing pressure (salp swarms). As the opposite was true for the PFr, large phytoplankton blooms developed. However, blooms were found only in association with the Polar Front but not the other fronts covered by this cruise. Why no significant biomass build-up occurred in the region of the southern fronts, despite the presence of the MIZ, could be attributed to frequent deep mixing by passing storms in conjunction with low iron concentrations. However, grazing pressure by metazooplankton seemed to be significantly lower than in the sACC, and, as discussed next, it is difficult to identify a single most important factor responsible for suppressing biomass build-up in the MIZ.

The weather regime during the investigation period was characterised by a stable high-pressure zone north of the Polar Front and the intermittent passage of low-pressure systems—at roughly weekly intervals—along the sACC. The resultant deep mixing could well have counteracted the stratifying influence of the MIZ and suppressed biomass build-up. However, calm weather conditions prevailed along the MIZ during at least 10 days in October while the west–east transect was being carried out. None the less, higher chlorophyll concentrations were only encountered in the area influenced by the Peninsula; throughout the region East of about 40°W, biomass levels were monotonously low (Bathmann *et al.*, 1997). Further, the presence of sea ice is known to dampen wave action and hence vertical mixing (Sullivan *et al.*, 1988); thus, periods between storms should have sufficed to boost phytoplankton stocks significantly, but this did not occur. Hence, it appears unlikely that bouts of stormy weather alone were responsible for maintaining low phytoplankton stocks at the MIZ. Further, the PFr blooms were very sharply delineated from adjoining waters of the sACC. If wind mixing was the determinant factor, then the northern, calmer stretches of the sACC (as compared to the southern parts) should have had higher biomass, contrary to observations.

An apparently more important factor is the difference in mesoscale dynamics between the two frontal regions. This becomes apparent from a comparison of the isopycnals recorded during the three major transects along 6°W (Veth *et al.*, 1997). Whereas the Polar Front underwent considerable meandering and latitudinal displacement of mesoscale water masses, the AWB front remained stationary and sharply demarcated by steep isopycnals throughout the investigation period. Strong vertical movement of water layers also was observed at the AWB, which would have had a detrimental influence on biomass build-up. Veth *et al.* (1997) argue that the difference in hydrography between the two frontal regions was driven by corresponding differences in bottom topography. At this

stage the effect on phytoplankton populations is far from clear and certainly warrants closer study.

A mixing depth shallower than about 50 m is considered a prerequisite for bloom build-up (Sakshaug and Holm-Hansen, 1984; Smetacek and Passow, 1990; Mitchell and Holm-Hansen, 1991). However, as discussed below, open-ocean blooms, including those we found in the PFr, tend to extend to much greater depths. Dieckmann (1987) reported phytoplankton standing stocks (*ca* 90 mg Chl *a* m^{-2}) at the AWB that were three-fold larger than in our study but further to the east, in the vicinity of the Greenwich Meridian. His observations are all the more surprising as they were made in early September, a time when the ice edge was advancing. Peak values were located just north of the ice edge at 57°S, but chlorophyll concentrations above 0.5 mg Chl *a* m^{-3} extended as far south as 59°S (Dieckmann, personal communication, 1996). Throughout the high biomass region, chlorophyll concentrations were homogeneous down to at least 100 m depth and deeper. These observations suggest that the minimum light requirements for accumulation of significant biomass levels (i.e. above 0.5 mg Chl *a* m^{-3}) in terms of mixed layer depth and irradiance might be less than currently believed. Of course, one also has to consider loss rates, but this aspect is dealt with further below.

A question that arises is why biomass levels at the AWB remained so low during our study if blooms can develop there in early September. Scharek *et al.* (1994) found low chlorophyll concentrations (0.2 mg Chl *a* m^{-3}) in the same region and a month later than Dieckmann (1987). On the return transect of the same cruise, Scharek *et al.* (1994) also failed to observe biomass build-up at the melting ice edge along the AWB in early December, despite shallow salinity stratification. These observations, carried out in the same year, suggest that blooms are episodic and ephemeral and occur independently of the retreat of the ice edge. Alternatively, there are marked interannual variations in timing or even occurrence of blooms, possibly driven by the stochasticity of iron input.

A major finding of our study is that input of meltwater and associated ice algae to the surface layer from a retreating ice edge is by itself an insufficient condition for the induction of phytoplankton blooms. This observation is supported by the results of the U.K.-JGOFS study carried out in November/December 1992 in the Bellingshausen Sea which demonstrated that the retreating ice edge had little effect on phytoplankton biomass distribution (Turner *et al.*, 1995). The large diatom bloom encountered in that study—about double the standing stock found by us in the PFr—was located in a frontal region at 67°–68°S and extended to a depth of 70 m. The physical conditions that enabled the build-up of such a large standing stock in a deep water column could not be ascertained from that study (Savidge *et al.*, 1995). Indeed, the developmental dynamics of deep frontal blooms such as those observed by us in the PFr and by Dieckmann (1987) in the AWB cannot be satisfactorily explained with the available data.

Diatom blooms in the PFr

Growth stimulation by the high iron concentrations throughout the PFr is an important factor for bloom development. Nevertheless, the abundant supply of iron did not lead to full utilisation of macronutrients and other factors such as, for example, suboptimal light are also significant at the PFr (de Baar *et al.*, 1995). Whereas this would apply to the PFr as a whole, it does not explain the differences in dominance status of the species comprising the three blooms. These evidently developed in distinct mesoscale water masses that were

related to meandering of the Polar Front and had experienced different past histories. The zonal extent of the mesoscale structures could not be ascertained but the fact that the dominant species *Fragilariopsis kerguelensis* and *Corethron criophilum* retained the positions of their peaks relative to one another in the PFr in the 3 weeks between Transects 5 and 11 suggests a band-like structure along the Polar Front. Similar dominance patterns were reported by Laubscher *et al.* (1993).

Both these species are widely distributed in the Southern Ocean (Savidge *et al.*, 1995), so their respective dominance in the water masses can not be attributed to differences in seeding stocks. Further, in view of their comparatively low concentrations relative to the abundant ambient nutrients, including iron, and the basically similar light climate across the PFr, one can hardly invoke competitive exclusion to explain dominance status. Species-selective loss rates, i.e. lower mortality of the dominant species relative to the others, while assuming similar growth rates, also must be considered. There was little evidence for this, as grazing pressure was low and the grazers involved are not known for their selective feeding behaviour (Klaas, 1997). Rather, the evidence points to selective stimulation of growth rates of certain species in their respective water masses. This would imply that, whatever the nature of the factors inducing bloom development, they occur in combination and have a selective impact by favouring the growth of some species relative to others. The patchy nature of the biomass peaks and the sharp gradients between species-specific patches support this view. It follows that a suite of factors must be at work for the induction of frontal diatom blooms, and we speculate that these vary between mesoscale water masses forming along the frontal region.

Although chlorophyll concentrations in the PFr are modest compared to neritic blooms, the standing stock maxima attained (177–277 mg Chl *a* m^{-2}) are indeed very high when compared with other oceans. Thus, the N. Atlantic spring bloom at a comparable latitude (47°N; 20°W) increased from 50 to 160 mg Chl *a* m^{-2} during 3 weeks (Lochte *et al.*, 1993). The much higher standing stocks found in the PFr were due to the much deeper extension of the blooms (> 70 m) as compared to those from other areas.

Shelf blooms, but also the N. Atlantic spring bloom, tend to be terminated by exhaustion of a major nutrient. Both nitrate and silica exhaustion are reported to trigger mass aggregation and sedimentation of diatom blooms (Smetacek, 1985). Although the northern rim of the PFr might well have experienced Si exhaustion later on in the season, it is unlikely that this occurred throughout the PFr. Light deprival does not seem to have had a similar effect either, as indicated by the deep extension and persistence of the chlorophyll maxima, which also points to a low overall mortality. Hence mass sedimentation of the blooms in the PFr or rapid decimation due to heavy grazing appears unlikely. Rather, although the fate of the biomass of the PFr blooms remains to be ascertained, it is likely to differ from that of the North Atlantic where rapid sinking of the bloom and subsequent formation of a layer of fluff on the sea bed have been reported (Lampitt, 1985; Lochte *et al.*, 1993).

Mass sinking of silica cell walls in the *Corethron* bloom following initiation of sexual stages is a previously unreported mechanism that reduces population size and induces vertical flux (Crawford, 1995). Such events are suggested to lead to the monospecific layers of this diatom found in some sediment cores from the Weddell Sea. This example illustrates how the biology of a dominant organism can, by retaining organic matter and exporting silica, exert a unique influence on magnitude and composition of vertical flux. The other dominant diatom in the PFr, *Fragilariopsis kerguelensis*, is a major contributor to the silica girdle underlying the ACC. However, very little is known about its life cycle and the fate of

its blooms. Verity and Smetacek (1996) have argued that elucidating the life cycles and behaviour of such "work-horse species" will significantly further our understanding of ocean biogeochemistry.

Drawdown of CO_2 was found in association with the PFr blooms. The PFZ is also the site of formation of Antarctic Intermediate Water (AAIW). This regional uptake via the "biological pump", however, is counteracted by a simultaneous outgassing of CO_2 rich water at the sACC–sF–Weddell Gyre region due to seasonal warming following sea-ice retreat when winter-accumulated, excess CO_2 is exposed to the atmosphere. Overall, the 1000 km long section studied during the spring represented a minor net sink for atmospheric CO_2. The large seasonal and regional variations of underlying physical and biological processes as yet precludes extrapolation to an annual basin-wide estimate of air–sea exchange of CO_2.

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APPENDIX

Size-fractionated primary production in the open Southern Ocean in austral spring. (F. J. Jochem, S. Mathot and B. Quéguiner (1995) *Polar Biology* **15**, 381–392).

Abstract—Size fractionated primary production was measured by carbon-14 uptake incubations on three transects between 47°S and 59°30′S along 6°W in October/November 1992. Open Antarctic Circumpolar Current and ice-covered Weddell Gyre water showed comparable low productivity (~ 0.3 g C m^{-2} day^{-1}) and size distribution. Picoplankton (< 2 μm) was the dominant size fraction, contributing approximately half to the total water column production. The significance of larger (> 20 μm) phytoplankton was only minor. Productivity in the Polar Front Zone north of 50°S, with higher water column stability, was up to 10 times higher with microplankton (> 20 μm) being predominant. No ice-edge bloom occurred over the 2-months study period; this is explained by non-favourable hydrographic conditions for blooming and the lack of melt-water lenses upon ice retreat. Picoplankton tended to be make higher contributions at lower water column stability, and microplankton to make higher contributions at higher stability. Mixing, together with light climate, is discussed as the driving forces for Antarctic primary production and for its size structure.

The role of sex in the sedimentation of a marine diatom bloom (R. M. Crawford (1995) *Limnology and Oceanography* **40**, 200–204).

Abstract—A longitudinal transect in the Atlantic sector of the Southern Ocean extending from the ice-covered Weddell Sea across the Antarctic Circumpolar Current and into the Polar Frontal Zone was studied repeatedly during the austral spring. The centric diatom *Corethron criophilum* was found at most stations in variable numbers, but in the Polar Frontal Zone I encountered a large bloom undergoing a mass sexual phase. This event apparently triggered downward transport of empty diatom cell walls in numbers that suggest the phenomenon is significant for the vertical silica flux and the formation of monospecific layers of this important diatom species in Southern Ocean sediments. Comparison of the cell-wall dimensions of such a monospecific layer with those in the plankton in the sexual phase reveals a characteristic signature that may indicate the provenance of these layers.

Importance of iron for phytoplankton blooms and CO_2 drawdown in the Southern Ocean (H. J. W. de Baar, J. T. M. de Jong, D. C. E. Bakker, B. M. Löscher, C. Veth, U. V. Bathmann and V. Smetacek (1995) *Nature* **373**, 412–415).

Abstract—The iron hypothesis—the suggestion that iron is a limiting nutrient for phytoplankton productivity and consequent CO_2 drawdown—has been tested by small-scale experiments in incubation bottles in the subarctic Pacific and Southern Oceans, and by a recent large-scale experiment in the equatorial Pacific Ocean. Here we test the idea by looking at natural levels of productivity in regions of the Southern Ocean with differing iron abundance. In the southerly branch of the Antarctic circumpolar current (ACC), upwelling of deep waters supplies sufficient iron to the surface to sustain moderate primary production but not to permit blooms to develop. In contrast, within the fast-flowing, iron-rich jet of the polar front (PF), spring blooms produced phytoplankton biomass an order of magnitude greater than in southern ACC waters, leading to CO_2 undersaturation. The plankton-rich PF waters were sharply delineated from adjacent iron-poor waters, indicating that iron availability was the critical factor in allowing blooms to occur.